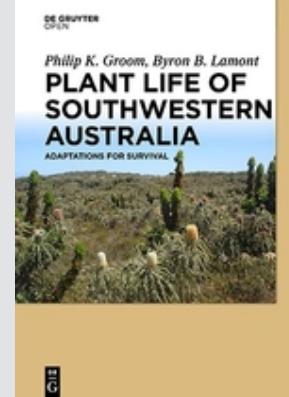


Philip K. Groom, Byron Lamont

PLANT LIFE OF SOUTHWESTERN AUSTRALIA

Adaptations for Survival



The southwestern Australian flora is unique in the world, not only for its biodiversity and endemism, but also for its functional biodiversity. It also contains the world's most nutrient-impoverished soils, has a prolonged-summer period and the vegetation is extremely fire-prone. These conditions have engendered an array of survival adaptations that have evolved in these harsh conditions across a diverse range of species. It is well recognised that the southwest flora has the toughest and most spiny vegetation of the world, the greatest number of species that store their seeds in woody fruits, and the most specialised means of obtaining limited soil nutrients and water.

This book focuses on the survival mechanisms, adaptations and ecology of the unique Southwest Australian flora (restricted here to flowering plants). The book begins with an examination of how the flora has evolved into the present forms. It describes further in detail the adaptive responses of the flora to the main environmental pressures influencing survival - fire, summer drought, nutrient-impoverished soils, pollination and seed dispersal agents. Specialised responses to obtain essential nutrients are presented in three chapters – carnivorous plants, parasitic plants and specialised roots. An entire chapter is devoted to leaves, with an insight into how leaves may assist in protecting flowers and fruits from herbivores and seed-eaters. The book provides an ecological perspective on how the flora has evolved complex strategies to ensure species survival in the relatively harsh seasonal climate of a Mediterranean-type ecosystem.

Survival Strategies, Mediterranean-Type Climate, Plant Biodiversity

Philip K. Groom and **Byron B. Lamont** are leading researchers in the ecology of the uniquely biodiverse southwestern Australian flora.

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8 Pollination Syndromes

The vast majority of species in the SouthWest flora requires animal visitors to their flowers to transfer pollen and promote outbreeding (known as zoophily) (Phillips *et al.*, 2010). However, major monocot families – the grasses (Poaceae), sedges (Cyperaceae) and wirerushes (Restionaceae) have abundant pollen that is solely wind dispersed (anemophily) and also have feathery stigmas that catch pollen. Anemophily also occurs in the dicot families of Sapindaceae (*Dodonaea*), Surianaceae (*Stylobasium*) and the fire ephemeral, Gyrostemonaceae (Keighery, 1981). For zoophilous species, flower colour, shape and size, and the amount of nectar produced are important determinants of the type of animal they attract, and in some cases they only utilize a single pollinator species (e.g. sexually deceptive orchids) (Table 8.1).

Table 8.1: Typical floral syndromes of the SouthWest flora that are adapted for pollination by insect, bird or mammal species.

	Insect	Bird	Mammal
			
Example	<i>Hypocalymma angustifolium</i>	<i>Banksia prionotes</i>	<i>Banksia nutans</i>
Anthesis	Diurnal, nocturnal	Diurnal	Nocturnal
Colour	Blue, white, yellow,	Red, yellow, green	Purple, brown, orange
Intensity	Bright	Bright	Dull
Position	Prominent	Prominent	Hidden
Inflorescence	Soft	Firm, wiry	Firm, wiry
Inflorescence size	Small	Large	Large
Nectar - volume	Small	Large	Large
- sugar content	Low	High	High
Odour	Strong (sweet)	Scentless	Strong (musky)

The variety of flower colours in the flora indicates appeal to a wide range of possible vectors. Insects (entomophily) are most sensitive to the ultraviolet and blue end of the light spectrum. Birds (ornithophily) are most sensitive to the red end and see in a similar range to humans.

For example, 75% of *Eremophila* species (Scrophulariaceae) are entomophilous with a protruding lower lip as a landing platform and are coloured blue, purple or white, while the remainder are ornithophilous with the lower lip depressed away from the throat with exserted stamens and style and are red, orange, yellow or green (Chinook, 2007). Mammals see in a similar range to humans but rely much more on their strong sense of smell, unlike birds. Thus, three basic pollination syndromes may be recognized in the SouthWest flora (Table 8.1).

8.1 Insect-pollinated Species

The range of insect pollination strategies occurring within the SouthWest flora is provided in Table 8.2., with examples of insect-pollinated flowers in Fig. 8.1. The main insect pollinators of the SouthWest flora are hymenopteran (bees, wasps), dipteran (particularly bee flies, but also other flies, mosquitos, gnats), coleopteran (beetles, particularly scarab beetles; Fig. 8.2) and lepidopteran (butterflies, moths) species. In this book we highlight the possible coevolutionary responses of plants to native bees and wasps.

8.1.1 Case Study: *Grevillea leucoptera*s

*Grevillea leucoptera*s (Proteaceae) has all the characteristics of a species pollinated by night-active insects (Fig. 8.2) including emitting a musky odour and the production of copious nectar at dusk that peaks by midnight (Lamont, 1982c). Giant scarab beetles (*Pachytricha* spp.: Melolonthidae) are lured to the plants from great distances by the smell and then guided by the white flowers that stand out against the dark sky. As they probe for nectar they spring open the flowers, whose turgidity greatly increases at nightfall, and pollen brushes against their thorax and wing covers. Many moths are also attracted but they are ineffective as pollinators, while crickets and honey possums are effective but poorly mobile by comparison. *G. leucoptera*s is self-compatible and spontaneous autogamy and geitonogamy may still result in seed set if xenogamy fails.

Table 8.2: Summary of floral characteristics of entomophilous pollination subcategories (adapted from Armstrong, 1979)

Syndrome	Colour range	Structure	Access to reward	Odour	Species examples
Canthiphily (beetle pollinated)	Dull coloured; white-cream	Flowers facing upward, or landing platform provided	Easy. Reward usually pollen rather than nectar	Strong – fruity/ spicy	<i>Cyanicula gemmata</i> (Orchidaceae) <i>Hibbertia hypericoides</i> (Dilleniaceae) <i>Philothea</i> spp. (Rutaceae)
Myophily (flies or gnat pollinated)	Various colours; pale or dull	Depends on pollinator mouthpart length	Easy	Nil or strong – foul smelling	<i>Pterostylis</i> spp. (Orchidaceae) <i>Monotoca tamariscina</i> (Ericaceae) <i>Leucopogon verticillatus</i> (Ericaceae) <i>Hakea denticulata</i> (Proteaceae) <i>Grevillea gordoniana</i> (Proteaceae)
Melittophily (bee pollinated)	White, cream, yellow, blue, purple	Deep and robust; held terminally on flowering stems in clusters or singularly in axils	Difficult, often conce- aled	Nil or slightly sweet	<i>Verticordia nitens</i> , <i>V. aurea</i> (Myrtaceae) <i>Conostephium pendulum</i> (Ericaceae) Fabaceae (many spp. in the three subfamilies) <i>Conospermum</i> spp. (Proteaceae) <i>Micratia parviflora</i> (Orchidaceae)
Myrmecophily (ant pollinated)	Various colours; Pale or dull	Small, clustered, usually close to the ground	Easy or no reward	Nil	
Sphecodiphily (wasp pollinated)	Dull, non-descript	Single blooms terminal on flowering stems. Structure unique to specific pollinator	No reward; or if present easily acces- sible	Nil (may emit phe- romones to attract a male wasp)	<i>Drakaea</i> spp. (Orchidaceae) <i>Cryptostylis</i> spp. (Orchidaceae) <i>Darwinia diosmoides</i> , <i>D. pauciflora</i> (Myrtaceae) <i>Hemianthus pungens</i> (Lamiaceae)
Phalaenophily (moth pollinated)	Pale-white, cream, or dull red	Pendulous or held at angle	Difficult. Long distance to nectar source	Strong, sweet	<i>Lysinema ciliatum</i> , <i>L. elegans</i> (Ericaceae)
Psychophily (butterfly pollinated)	Pink, magenta-red. Vivid colouring	Terminal and erect. Medium sized single flowers or clustered small flowers	Difficult. Long distance to nectar source	Nil, or subtle	<i>Calytrix</i> spp. (Myrtaceae) <i>Pimelea</i> spp (Thymelaeaceae)



Grevillea gordoniiana
(Proteaceae) with blowfly



Scaevola species
(Goodeniaceae)



Acacia pulchella
(Fabaceae)



Hibbertia hypericoides
(Dilleniaceae)



Rhodanthe chlorocephala
(Asteraceae)



Melaleuca robusta
(Myrtaceae)



Verticordia acerosa
(Myrtaceae)



Banksia lemanniana
(Proteaceae) with *Cryptochilellus*
wasps



Viminaria juncea
(Fabaceae)

Fig. 8.1: Examples of the taxonomic, structural and colour diversity within insect-pollinated flowers in the SouthWest flora.

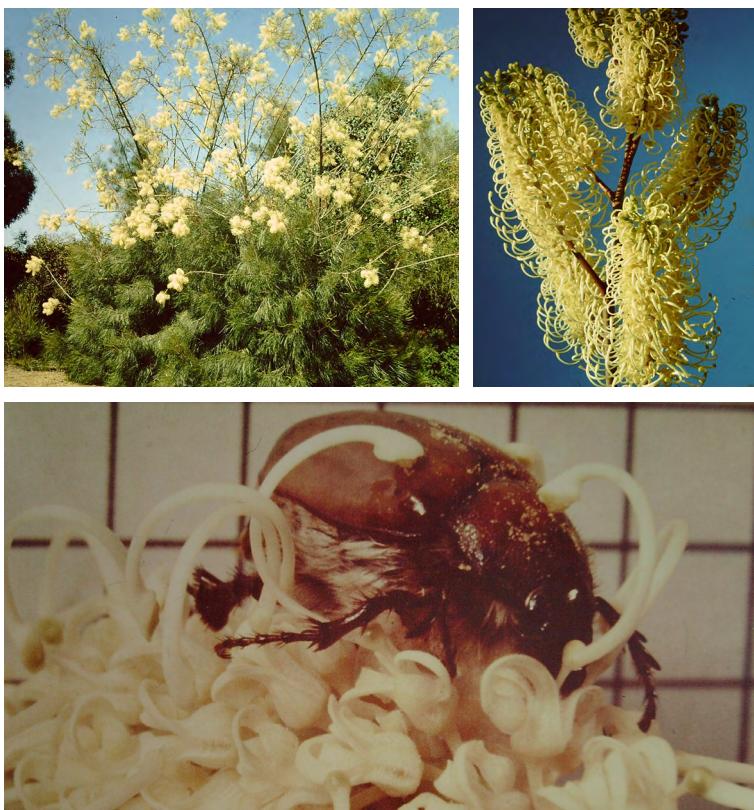


Fig. 8.2: *Grevillea leucoptera* has all the characteristics of a species pollinated by night-active insects. (*upper left*) two plants with naked scapes holding thousands of white flowers during spring up to 4 m above the scrub-heath in the northern sandplains. (*upper right*) Flowers in terminal panicles of racemes, 8-12 cm long, open towards the apex suggestive of an adaptation to flying pollinators. (*lower*) Giant scarab beetles, *Pachytricha* spp., 4 cm long, are the main pollinators.

8.1.2 Bee Pollination

Hymenopteran species, primarily bees, tend to visit only one flower type to obtain pollen and/or nectar, using scent and visual cues (Chittka *et al.*, 1999). Floral colour properties, revealed by their spectral reflectance, have a close affinity with the ability of bees to visualize and discriminate colour patterns (Dryer *et al.*, 2012). Because this synergy exists in both the Northern Hemisphere and Australian floras independently, it is hypothesized that bee visual adaptability has been a major evolutionary driving force for the rapid speciation and radiation of Australian, insect-pollinated, angiosperm taxa (Dryer *et al.*, 2012). Australia has a high number of species in the bee family Colletidae (Batley & Hogenboorn, 2009) an ancient group

of bees with Gondwanan origins that evolved during the Cretaceous (72–82 Ma) with an accelerated period of radiation worldwide commencing during the Oligocene and Neogene (Almeida *et al.*, 2012). The Australian endemic subfamily Euryglossinae and the Australian biodiverse subfamily Hylaeinae both evolved 48–54 Ma. Bee pollination (melittophily) is considered an ancestral trait in the tribes Mirbeliae and Bossiaeae (Fabaceae) (Toon *et al.*, 2014), Haemodoraceae (Hopper *et al.*, 2009), Australian Ericaceae (Johnson, 2012), Myrtaceae (Lughadha & Proenca, 1996) and several other families.

Many native SouthWest bees adapt either morphologically or behaviourally to their food sources, or at least trade-offs between bee and floral characteristics exist that allow the development of exclusive plant-pollinator relationships. They may visit a taxonomically-diverse range of flowers or specifically visit plants in the same genus (oligolectic) or just a particular species (monolectic). Bees of the Australian endemic *Euryglossa* (Colletidae) are considered important pollinators of the Myrtaceae (Exley, 2004). The oligoleptic *Euryglossa tuberculifera* accesses nectar from the predominantly bird-attracting *Calothamnus* (Myrtaceae) flowers (see Fig. 8.11) because of its enlarged mouth-feeding parts that join to form an elongated tube (Houston, 1983), whereas the monolectic *E. semaphore* only visits the pink-flowered *Pileanthus filifolius* (Houston, 1992). Twenty *Euryglossa* species seem to have adapted to feeding from blue-violet-flowered *Eremophila* (Scrophulariaceae) species through enlarged labial palps and longer heads (Exley, 1998); thus euryglossin bees are not exclusive pollinators of the Myrtaceae. Bee species from the megachilid genus *Chalicodoma* have been observed visiting the pink flowers of *Calytrix fraseri* (Myrtaceae) (Hawkeswood, 1993), a species that has floral features associated with butterfly pollination (Morcombe (1968) has an image of a butterfly visiting *C. fraseri*).

Verticordia (Myrtaceae) flowers have a special affinity with bees as well as flies and beetles (Hawkeswood, 1993; Houston *et al.*, 1993; Exley, 2004), and occasionally are adapted for honeyeater pollination (e.g. *V. grandis*, *V. staminosa*). Table 8.2 lists some of the bee species known to visit *Verticordia* flowers. Many of the euryglossin *Dasyhema* are associated with different species of *Verticordia* resulting in the recognition of new species of this bee (Exley, 2004). Some are named after the *Verticordia* they are associated with (e.g. *D. spicata* visits *V. spicata*) (Table 8.3). This does not necessarily imply that these *Dasyhema* are exclusive pollinators of their associated *Verticordia*. For example, although *D. forrestii* has been recorded visiting only *V. forrestii* flowers (Exley, 2004) the jewel beetle, *Castiarina forrestii* (Buprestidae), is also a visitor (Bellamy *et al.*, 2013). Flowers of *V. nitens* and *V. aurea* have hooded anthers with a terminal spout that releases a pollen-oil mixture (Houston *et al.*, 1993; Fig. 8.3). Each species is exclusively pollinated by the euryglossin bees *Euryglossa morrisonii* and *E. aureophila* respectively (Houston, 1992; Houston *et al.*, 1993).



Fig. 8.3 *Verticordia* (Myrtaceae) is an advanced genus with highly modified flowers in a family that stretches back 65 million years. All but two of the known 104 species are endemic to the SouthWest (George & Pieroni, 2002; George & Barrett, 2010). (*lower left*) *V. nitens* is a slender shrub that appears top heavy because of the broad surfaces of brilliant orange flowers (corymbs) it produces in early summer atop a thin main stem, 0.5–1.75 m tall. This species is locally abundant in the understorey of banksia low woodland of the Swan Coastal Plain. The corymbs act like a single large flower (pseudanthium) as a device for enhancing attractiveness to pollinators, serving as a landing platform and facilitating movement from one flower to the next. Unlike many other oligolectic verticordias that present their pollen to visitors (Lamont, 1985a), *V. nitens* has a specialist pollinator (monolectic), a tiny solitary bee, *Euryglossa morrisoni* (Colletidae), that is entirely reliant on this verticordia for its nutrition (Houston *et al.*, 1993). (*upper left*) a female bee squeezing the hood of an anther with its mandibles and lapping up the pollen–essential oil mix from the terminal spout through which it is released. Note globs of pollen on its head and thorax. Flowers, 8 mm wide, with their highly reflective petals and hypanthium make the specific name, *nitens* (latin for shining) most appropriate. (*upper right*) a male bee lapping up nectar from the floor of the hypanthium and receiving oily pollen or brushing pollen onto the central stigma. (*lower right*) Scanning electron micrograph showing individual flower of *V. nitens* with its 10 fertile stamens: h = helmet cover over anther, s = spout through which oily pollen is passed to the bee. The dearth of nectar and the inaccessibility of both nectar and pollen appear to explain the lack of visits by larger pollinators and nectar robbers. In the absence of *E. morrisoni*, seed set is negligible.

Table 8.3: Australian native bees recorded as visiting *Verticordia* species. Data provided where both *Verticordia* and bees were identified to the species level. Information obtained from the Australian Bee Pollination Index Query database via the Victorian Museum website, www.museum.vic.gov.au. Accessed 15 August 2014.

Verticordia species	Bee species	Bee Family
<i>V. argentea</i>	<i>Dasyhesma argentea</i>	Colletidae
<i>V. aurea</i>	<i>Euryglossa aureophila</i>	Colletidae
<i>V. chrysanthia</i>	<i>Paracolletes nigrocinctus</i>	Colletidae
<i>V. chrysanthia</i>	<i>Stenotritus greavesi</i>	Stenotritidae
<i>V. chrysanthia</i>	<i>Ctenocolletes smaragdinus</i>	Stenotritidae
<i>V. densiflora</i>	<i>Exoneura nigrescens</i>	Apidae
	<i>Exoneura pictifrons</i>	Apidae
	<i>Hylaeus rufipes</i>	Colletidae
	<i>Paracolletes callander</i>	Colletidae
	<i>Paracolletes nigrocinctus</i>	Colletidae
	<i>Lasioglossum sculpturatum</i>	Halictidae
	<i>Lasioglossum lichatum</i>	Halictidae
	<i>Lipotriches australica</i>	Halictidae
	<i>Lipotriches flavoviridis</i>	Halictidae
	<i>Megachile rugosa</i>	Megachilidae
	<i>Ctenocolletes smaragdinus</i>	Stenotritidae
<i>V. densiflora</i> var. <i>cespitosa</i>	<i>Ctenocolletes albomarginatus</i>	Stenotritidae
<i>V. dichroma</i> var. <i>dichroma</i>	<i>Euryglossa evansi</i>	Colletidae
	<i>Dasyhesma simulata</i>	Colletidae
<i>V. dichroma</i> var. <i>syntoma</i>	<i>Dasyhesma galbina</i>	Colletidae
	<i>Dasyhesma syntoma</i>	Colletidae
<i>V. forrestii</i>	<i>Dasyhesma forrestii</i>	Colletidae
<i>V. huegelii</i>	<i>Paracolletes nigrocinctus</i>	Colletidae
<i>V. lepidophylla</i> var. <i>quantula</i>	<i>Dasyhesma lepidophyllae</i>	Colletidae
<i>V. muelleriana</i> subsp. <i>muelleriana</i>	<i>Dasyhesma muelleriana</i>	Colletidae
<i>V. nitens</i>	<i>Euryglossa morrisonii</i>	Colletidae
<i>V. oculata</i>	<i>Dasyhesma areola</i>	Colletidae
<i>V. pholidophylla</i>	<i>Amegilla cingulata</i>	Apidae
<i>V. picta</i>	<i>Paracolletes nigrocinctus</i>	Colletidae
	<i>Ctenocolletes albomarginatus</i>	Stenotritidae
	<i>Ctenocolletes smaragdinus</i>	Stenotritidae
<i>V. plumosa</i>	<i>Thyreus waroonensis</i>	Apidae
	<i>Paracolletes nigrocinctus</i>	Colletidae
	<i>Leioproctus velutinellus</i>	Colletidae
<i>V. polytricha</i>	<i>Euryglossa evansi</i>	Colletidae
<i>V. pritzelii</i>	<i>Lasioglossum instabilis</i>	Halictidae
<i>V. serrata</i> var. <i>serrata</i>	<i>Euryglossa lucida</i>	Colletidae
<i>V. spicata</i>	<i>Dasyhesma spicata</i>	Colletidae
<i>V. stenopetala</i>	<i>Ctenocolletes smaragdinus</i>	Stenotritidae

Anther morphology and function in *Verticordia* was surveyed by Ladd *et al.*, (1999) who recognized three main anther types, with and without oil-producing glands. Not all oil-producing anthers are hooded like *V. aurea* and *nitens*, and there is some relationship within subgenera between the type of pollen presenter and the presence of anther glands. In a study of *Verticordia* pollen morphology, Thornhill *et al.* (2012) noted that pollen with very small colpi (elongated apertures) are more likely to be associated with anther oil-production. No doubt anther modifications are the result of natural selection for maximizing pollen transfer, and thus there are potentially numerous monolectic melittophilous relationships occurring within *Verticordia* many of which we are currently unaware. Pollen structure is unusually variable within the mostly entomophilous *Conostylis* (Haemodoraceae) (Pierce & Simpson, 2009) and has adaptive implications for evolution of pollinator selection over the 14 million years of *Conostylis* existence (Hopper *et al.*, 2009).

Another colletid genus, *Leioproctus*, is an important bee pollinator of the SouthWest flora. Three species (*L. conospermi*, *L. pappus* and *L. tomentosus*) are cryptic obligate feeders on *Conospermum* (Proteaceae) flowers (Houston, 1989) with mouthpart modifications enabling these species to cope with *Conospermum*'s explosive pollen release. In contrast, the monolectic *L. macmillanii* has an unusually elongated head that enables access to nectar of the floral-tubed *Astroloma xerophyllum* (Ericaceae) (Houston, 1991). *Leioproctus* has also been observed visiting the buzz-pollinated pendulous and nectarless flowers of *Conostephium* (Ericaceae) (Houston & Ladd, 2002). Buzz pollination is unusual in this genus because the anthers are not physically available to visiting bees. Instead the sonified vibrations are transferred to the anthers *via* the tapered purple corolla tube for pollen release (Houston & Ladd, 2002).

Buzz pollination occurs in species that require the rapid vibration of the anthers (known as sonication) to release pollen, and is performed exclusively by native bees. Buzz-pollination is a common feature not only of *Conostephium* but also *Coleanthera* (Ericaceae) (Houston & Ladd, 2002), *Hibbertia* (Dilleniaceae) (Tucker & Bernhardt, 2000), *Dianella* (Hemerocallidaceae) (Duncan, Cunningham & Nicotra, 2004), *Solanum* (Solanaceae), *Thysanotus* (Anthericaceae) (Fig. 7.12) and *Tetratheca* (Elaeocarpaceae).

Hibbertia species (Fig. 8.2) are pollinated by female pollen-collecting bees (Colletidae and Halictidae), scarab beetles (Scarabaeidae) and pollen-eating flies (Syrphidae), with four pollination syndromes recognised in the genus that are based on flower size and symmetry (Tucker & Bernhardt, 2000).

8.1.3 Orchid Pollination

The Orchidaceae is exclusively entomophilous, and many SouthWest orchid species are pollinated by a specific insect species. Four pollination-attracting strategies are recognised in South West orchids, and outlined in detail in Table 8.4 and Fig. 8.4:

These are:

1. Nectar-producing flowers with diverse pollinators (low specificity)
2. Flowers that mimic flowers of other species but are themselves non-rewarding (medium specificity)
3. Winter-flowering species that attract fungus-feeding insects (high specificity)
4. Sexually deceptive—parts of the flower mimic female insects (very high specificity)

Table 8.4: Pollination strategies of southwestern Australian orchids (after Brundrett, 2007).

	Low specificity	Medium specificity	High specificity	Very high specificity
Pollinated by	Diverse insect groups	Insects with similar food requirements	Similar insects in the same functional group	Single insect or several similar species
Mechanisms	Nectar/food reward, often scented	Flowers resemble those of species from other plant families (food deception) but with no reward	Fungus mimicry; entrapment	Sexual deception; orchid mimics a female insect in shape and scent (pheromones)
Insect groups	Beetle, bee, fly, wasp, gnat	Beetle, bee, bee-fly, wasp	Fungus gnat, phorid fly, mosquito	Thynnine wasp, Ichneumonid wasp, ant
Representative genera	<i>Cyrtostylis</i> , <i>Microtis</i> , <i>Prasophyllum</i> , <i>Pyrorchis</i> , <i>Caladenia</i> (some), <i>Eriochilus</i> (some)	<i>Diuris</i> , <i>Caladenia</i> (~ 1/3 spp.), <i>Cyanicula</i> , <i>Eriochilus</i> , <i>Thelymitra</i>	<i>Corybas</i> , <i>Pterostylis</i> (most), <i>Rhizanthella</i>	<i>Caladenia</i> (~ 2/3 spp.), <i>Calochilus</i> , <i>Cryptostylis</i> , <i>Drakaea</i> , <i>Leporella</i> , <i>Paracaleana</i> , <i>Spiculaea</i>

An additional strategy that requires further evaluation are flowers with labellum projections mimicking stamens or pollen-laden anthers. This may occur in *Hyperanthus*, *Praecoxanthus* (Fig. 8.4) and some species of *Cyanicula*, with the deception being a visual cue for what is perceived as presence of a reward that attracts native bees as they approach the flower.



Fig. 8.4: *Praecoxanthus aphyllus* (upper left) emits a fragrant floral scent that predominantly attracts bees and prominent yellow calli on a purple and green labellum that superficially resemble pollen-bearing stamens. Flower is 4 cm wide. *Lyperanthus serratus* (upper right) is characterised by dense white calli that also superficially represent stamens. Flower is 5 cm wide. (lower left) *Ericksonella saccharata*, once classified as a *Caladenia*. Little is known about the pollination of this monotypic species. Flower is 2 cm wide. (lower right) *Eriochilus scabrus* is probably food deceptive and attracts native bees. Flower 3 cm wide. *Ericksonella* image provided by Esperence Wildflowers. All other images provided by Mark Brundrett.

Some species are obligatory self-pollinators (e.g. *Theelymitra vulgaris*, *Microtis media*, some *Calochilus* species) with flowers open for a few hours. *M. media* subsp. *densiflora* can produce up to 150 densely-packed flowers on a flowering spike, with open, fertilized and in-bud flowers co-occurring (Hoffman & Brown, 2011).

Within the Orchidaceae, the radiation and evolutionary transitions between pollinator strategies (reward vs deception) and rewards offered (nectar/food reward or no reward) occur independently across evolutionary lineages (Jersáková *et al.*, 2006; Johnson *et al.*, 2013). It is generally recognised that providing no nectar reward is an ancestral condition in orchids (Jersáková *et al.*, 2006) and that evolutionary shifts from deceptive to reward strategies implies adaptive responses to combat pollinator limitation issues relating to pollen dispersal and fecundity. Also the shift from food to sexual deception may be driven by selection for more efficient pollination, without compromising the high levels of gene flow that are characteristic of deceptive

species (Scopece *et al.*, 2010). To further understand the evolutionary and ecological significance of pollinator syndromes in SouthWest orchids, more comparative studies on how obligate self-pollination, food reward, food deceptive, and sexual deceptive strategies function within a phylogenetic framework are required.

8.1.3.1 Food Rewards

Orchid taxa that produce nectar as food reward are often scented and brightly coloured to attract frequent insect visitors, thus maximising the opportunities for pollen dispersal and pollination to occur including increased probability of selfing via geitonogamy. Flower size restricts the type of insect that can access the sweet nectar, an adaptation to prevent wastage and target beneficial pollinators.

Prasophyllum flowers are highly nectariferous and encourage visits by nectar-seeking beetles, flies, wasps and bees (Bernhardt & Burns-Balogh, 1986a; Elliott & Ladd, 2002) (Fig. 8.5). The related genus *Microstis* attracts small wingless ants, wasps, weevils and small flies (Peakall & Beattie, 1991; Hoffman & Brown, 2011) that visit for a nectar reward, whereas *Cyrtostylis* produces minute flowers that are pollinated by micro-flies. *Prasophyllum*, *Microstis* and *Cyrtostylis* species may have extremely small flowers (< 3 mm in length; Fig. 8.5) that attract micro-insects, with larger flowers (up to 25 mm long) only occurring within *Prasophyllum*. The monotypic SouthWest endemics *Leptoceras menziesii*, *Ericksonella saccharata* (Fig. 8.4) and some of the non-endemic genus *Eriochilus* may all fit into the food reward category, and all have white or purple perianth parts that act as attractants to native bees.



Fig. 8.5: (left) *Cyrtostylis robusta* produces nectar in a small reservoir at the base of the long, pointed labellum that runs down a narrow central groove and entices microdiptera (Hoffman & Brown, 2011). Flower length 15 mm. (right) *Prasophyllum regium* flowers are upside down (labellum faces upwards) and up to 25 mm long (Hoffman & Brown, 2011) and in this image a flower is being visited by a wasp. *Prasophyllum* image provided by Mark Brundrett. *Cyrtostylis* image courtesy of Esperance Wildflowers.

8.1.3.2 Pollinator Deception

Pollinator deception (also known as food deception) is considered to be an evolutionarily stable strategy within the Orchidaceae (Jersáková *et al.*, 2006). It is an important driver of floral and species diversity within the Orchidaceae, with food-deceptive orchids speciating at a much slower rate than sexually-deceptive orchids (Cozzolino & Widmer, 2005). Floral mimicry, or floral deception, may be modelled on mimicking one species or a suite co-flowering species, or attracts pollinators with commonly occurring colours, markers and scent (Schiestl, 2005).

Dafni & Bernhardt (1990) placed food deception into three groups. Generalist deception does not mimic a co-occurring model and thus attracts generalist insect foragers that will visit a range of co-flowering species. Floral mimicry occurs where the orchid flower mimics an individual, or a guild of related, taxa and is pollinated by insects that visit it. The third category is where the orchid flowers at the same time as unrelated species that offer nectar and/or pollen rewards to pollinators that the orchid can utilise. Food-deceptive orchids attract a guild of local insect pollinators, taking advantage of potential pollinator availability despite the risk of pollinator competition for pollinator visits. There is potential for co-occurring food deceptive orchids to share pollinators and thus increase the chance of natural hybrids occurring.

Caladenia contains species with two pollination strategies – food deception and sexual deception (Stoutamire, 1983; Phillips *et al.*, 2009). Food deceptive caladenias may be brightly coloured (e.g. *C. flava*, *C. latifolia*, Fig. 8.6) or dull (*C. bicalliata*), are nectarless and have some capacity to self-pollinate, suggesting that this is a strategy to ensure pollination occurs in the absence of visiting pollinators (Phillips *et al.*, 2009). It is proposed that food deceptive caladenias are not mimicking other species (non-model mimicry) as no other nectar rewarding taxa are morphologically similar in the SouthWest (Phillips *et al.*, 2009). Like the rewarding strategy, food deception may be viewed as evolutionary responses to overcome pollen limitations arising from infrequent pollinator visits and to maximise visitations between clonal plants.

The SouthWest endemic and monotypic *Praecoxanthus aphyllus* attracts native bees by a highly fragrant scent (Hoffman & Brown, 2011) and the display of a predominantly purple labellum with yellow calli on a purple and green labellum that partially resemble pollen-bearing stamens (pseudoandroecia) (Fig. 8.4). *Praecoxanthus* is said to be nectarless (M. Brundrett, *pers. comm.*) and probably utilises its pseudoanthers, coloured labellum and white perianth parts to attract visiting insects (thought to be mainly native bees) to an absent reward. Native bee pollination has been observed in *Pheladenia*, *Eriochilus*, and *Cyanicula* (along with beetles) (Hopper & Brown, 2004) and are potentially floral mimics, although the type of deception utilised has yet to be investigated. The relatively dull-coloured flowers of *Hyperanthus serratus* have been reported to produce nectar (Elliott & Ladd, 2002), but may be utilising their prominent and dense white calli at the apex of their labellum as a form of stamen mimicry to attract native bees (Fig. 8.4).



Fig. 8.6: (two upper rows) Flowers of *Caladenia flava* and *C. latifolia* offer food rewards to potential insect pollinators, in contrast to the sexually-deceptive flowers of *C. roei*, *C. discoidea*, *C. attingens* ssp. *atttingens* and *C. arenicola*. All sexually-deceptive *Caladenia* species are pollinated by thynnine wasps (Phillips *et al.*, 2009). Left image shows male *Phymatothynnus* wasps visiting flowers after being lured by sexually-deceptive volatile semiochemicals (as interpreted by Phillips *et al.*, 2009). (third row) *Prasophyllum* attracts insect pollinators with a sweet odour. Pictured is *Prasophyllum gracile*, the smallest member of the genus. Flowers are 5 mm in length. *Diuris longifolia* flowers (middle) utilise mimicry of co-occurring legume flowers (e.g. *Daviesia triflora*; right) to attract pollinators. (last row) The non-rewarding blue flowers of *Thelymitra crinita* appear to mimic native lilies (e.g. *Dianella*) or native irises (e.g. *Patersonia*). In contrast, the cream-flowered *T. antennifera* attracts pollinators of *Hibbertia* and *Goodenia* (Dafni & Calder, 1987; Bernhardt, 1995) – all radiate strongly in the UV range. *T. apiculata* (right) closely resembles the flowers of *Calectasia* (Dasypogonaceae). Flower is 3 cm wide. Images of *C. discoidea* and *T. apiculata* provided by Mark Brundrett. Image of *C. attingens* provided by Allen Lowrie.

For food deceptive *Thelymitra* species the deceit involves the mimicry of visual (flower colour) and olfactory (sweet odour) cues of co-occurring and co-flowering genera to attract male bees (Bernhardt & Burns-Balogh, 1986b; Dafni & Calder, 1987; Sydes & Calder, 1993). The blue flowers of the SouthWest endemics *T. crinita* (Fig. 8.6) and *T. macrophylla* resemble those of blue-flowered lilies (e.g. *Orthrosanthus laxus*, *Patersonia occidentalis*, *Stypandra glauca*) (Brown *et al.*, 2008). Studies on the chemical composition of floral fragrances emitted indicate that *T. macrophylla* is more closely mimicking *O. laxus* than does *T. crinita* (Edens-Meier *et al.*, 2014). Flowers of the *T. variegata* complex resemble those of *Calectasia* (Dasypogonaceae) (Fig. 7.18) although floral mimicry as a pollinator attractant has not been proven.

Diuris flowers are not usually sweetly scented nor do they offer a visiting insect any food reward. In *Diuris* the deception focuses on attracting a suite of pollinators from a guild of pea-flowered legumes (Fig. 8.6), thus increasing their evolutionary fitness by maximising insect visiting rates to reduce the risk of poor pollen transfer but increasing the potential for natural hybrids to occur between co-occurring species. Specifically the floral mimicry involves similarly coloured and shaped co-flowering peas (e.g. *Daviesia*, *Pultenaea*, *Isotropis*, *Gastrolobium*, *Gompholobium*) (Beardsell *et al.*, 1986; Indsto *et al.*, 2006; Brown *et al.*, 2008). Flowers of *Diuris purdiei* may mimic the shape, but not the colour, of co-occurring *Lobelia* (Campanulaceae).

Food deception in *Diuris* and *Thelymitra* has a moderate evolutionary cost because the requirements to select floral structures, colour, UV-guiding markers and positioning to precisely or generally mimic co-flowering species may be dependent on the evolutionary stability of floral traits and flowering periods of flowering species being mimicked. Mimicking flowers tend to be significantly larger than their models as a strategy to attract visiting insects at a short distance to the flowers after following a floral scent trail. This imperfect mimicry may not necessarily increase pollination success rates (Eden-Meier *et al.*, 2013).

8.1.3.3 Gnat Pollination

Other orchid genera attract fungus-eating gnats (e.g. *Corybas*, *Pterostylis* and *Rhizanthella*). *Rhizanthella gardneri* is a rare subterranean orchid restricted to two isolated populations in the SouthWest (Bougoure *et al.*, 2008; Chapter 6). Enlarged bracts (Fig. 8.7) that surround the underground inflorescence push through the top soil allowing the perfusion of a putrid odour that may mimic the scent emitted by fruiting bodies of mychorrizal fungi associated with the orchid's *Melaleuca* habitat.

Pterostylis flowers (Fig. 8.7) are complex traps that attract mosquitos and fungal gnats (Diptera). The labellum is hinged and moves in response to irritation by visiting insects that become trapped for 30–90 seconds inside the flower

between the labellum and the androgynoecious column (Bernhardt, 1995). The labellum then spontaneously resests itself, allowing the visiting insect to escape. *P. sanguinea* is visited by the male of a *Mycomya* (Mycetophilidae) gnat species (Phillips *et al.*, 2014) attracted by pheromone-like semiochemicals emitted from the flower's labellum.



Fig. 8.7: Fungal gnat pollinated orchids. *Rhizanthella gardneri* (upper) is obligately subterranean. Images of *C. discoidea* show that the tips of the enlarged fleshy bracts are the only part of the inflorescence that may protrude through the soil. In this image the soil surrounding the inflorescence has been removed to expose the 8-cm wide capitulum of deep red florets (6 mm in length), shown in close up on the right. (*lower*) *Pterostylis* (Greenhoods) often flower in autumn or winter when the gnats are most active (Brundrett, 2007). *P. angusta* (*lower left*; flower length 30 mm) has the longest labellum of all SouthWest greenhoods that protrudes between two upright fused sepals. (*lower right*) *P. barbata* (bird orchid), flower length 50 mm, has a characteristic translucent flower and sparsely fringed labellum. *Rhizanthella* (except close up of florets) and *P. angusta* images provided by Mark Brundrett. *P. barbata* provided by Allen Lowrie.

8.1.3.4 Sexual Deception

Sexually-deceptive orchids are the most pollinator-specialised plants in the SouthWest flora (Phillips *et al.*, 2010), a syndrome that has evolved multiple times in phylogenetically different orchid genera (Mant *et al.*, 2002; Hopper, 2009). It is a strategy that tricks male insects to pseudocopulate with the labellum in a way that promotes pollen transfer. Initially arriving after following a scent trail of volatile chemicals, males utilise visual cues such as colour and modified labellum parts to be lured to the flower.

Sexually-deceptive *Caladenia* species attract male thynnine wasps (Phillips *et al.*, 2009), with the plant-wasp relationship species-specific or the wasp may pollinate closely-related species (e.g. *Zaspilothynnus nigripes* and the *C. huegelii* complex) (Phillips *et al.*, 2009). The male is attracted to an orchid by the volatile semiochemicals (pheromones) that the flower emits from either the labellum, or glandular petal and sepal tips, and visual cues such as the dark calli on the labellum of *Caladenia roei* (Fig. 8.6) that mimic the female. In the subgenera *Calonema* and *Drakonorchis*, floral parts are highly engineered to attract their thynnine pollinators, including stiff and loose-hinged labellae.

Drakaea, *Paracaleana* and *Spiculaea* (Fig. 8.8) rely on sexual deception by males of different thynnine wasp species that pseudocopulate with the column, resulting in the transfer of pollinia between wasp and orchid, and their flowers are highly modified to achieve this (Fig. 8.8). Labella are terminated by an appendage that visually mimic a wingless female (called the pseudofemale). *Drakaea*, *Spiculaea* and some *Caladenia* (subgenera *Drakonorchis*) have bioengineered passive labella with soft and hard hinges that utilise the attempted copulation of an attracted male to propel the insect towards the column as a mechanism to transfer pollen. In *Drakea*, the labellum contains a delicate hinge that allows the labellum to swing backwards towards the upright column as the male wasp attempts to fly away with the pseudofemale. Within *Paracaleana* the labellum relies on slight pressure to bend the labellum stalk (or claw) downwards 180° toward the downward-pointing column (Hopper & Brown, 2006; Bower, 2014). Pollen transfer is only effective if male wasps are precisely positioned onto the labellal pseudofemale, and only a small percentage of visiting males effect transfer (Peakall, 1990).

There is a high level of pollinator specificity in *Drakaea*, with each species pollinated by males of different *Zaspilothynnus* (Thynnidae) species (Hopper & Brown, 2007; Manz *et al.*, 2013). Pollen movement is largely restricted to plants within populations (Menz *et al.*, 2013). Pollination studies of *D. glyptodon* show that, although the majority (93%) of visiting males *Z. trilobata* wasps landed on flowers, less than 21% held onto the pseudofemale with only 6% attempting to copulate in a way that would lead to pollen transfer (Peakall, 1990). Labella are elongated with the tip modified to imitate the body of female thynnine wasps (Fig. 8.8). Analysis of the volatile compounds emitted by *D. glyptodon* has revealed a blend of pheromone-like pyrazines as an important component of the attractant (Bohman & Peakall, 2014; Bohman *et al.*, 2014).



Fig. 8.8: Wasp pollinated orchids. All species emit pheromone-mimicking chemicals and have labella apices modified to resemble female wasp bodies. From top left to lower right: *Drakaea glyptodon* (hammer orchid), *Paracaleana triens* (flying duck orchid), *Cryptostylis ovata* (slipper orchid) and *Spiculaea ciliata* (elbow orchid). Except for *Cryptostylis*, all genera are pollinated by male thynnine wasp species within the genera *Zaspilothynnus* (*Drakaea*; Hopper & Brown, 2007), *Eirone* or *Thynnoturneria* (*Paracaleana*; Hopper & Brown, 2006, Peakall *et al.*, 2010; Bower, 2014) or *Thynnoturneria* (*Spiculaea*; Alcock, 2010). *Cryptostylis* is pollinated by the male ichneumonid wasp, *Lissopimpla excelsa* (Gaskell, 2012). Flowers vary in length from 20 to 30 mm. Images provided by Allen Lowrie.

By targeting only one pollinating species, sexually-deceptive orchids maintain floral isolation (Schiestl & Schlüter, 2009) that promotes outcrossing and causes lower fruit set than other pollination strategies (Jersáková *et al.*, 2006; Phillips *et al.*, 2009), although this is not always the case (e.g. *Cryptostylis*; Gaskell *et al.*, 2008). It also has the potential to result in increased pollen movement (Peakall & Beattie, 1996). Among endemic SouthWest *Drakaea*, pollen movement distances of up to 132 m (*D. glyptodon* (Peakall, 1990), 556 m (*D. elastica*) and 267 m (*D. lividia*) (Menz *et al.*, 2013) have been recorded, with pollen movement largely confined to within *Drakea* populations.

Hybridization in *Drakaea* is rare, occurring in mixed populations (Hopper & Brown, 2007), further supporting the secondary importance of colour mimicry and female wasp imitation for visits to occur. The evolutionary implications of extreme pollinator specialization will minimize the potential for hybridisation to occur,

particularly between small, isolated populations, but makes the species more prone to local and regional extinction if the pollinator population begins to decline (Phillips *et al.*, 2010). The success of sexual deception not only requires optimal searching and movement between flowering individuals by males, but also the presence of co-flowering species that offer a food reward.

The only sexually-deceptive species that does not attract male wasps is the monotypic *Leporella fimbriata* that sexually deceives winged male ants of *Myrmecia urens* (Formicidae: Myrmeciinae) (Peakall *et al.*, 1990, Peakall, 1989; Fig. 8.9). Growing clonally from underground tubers the species is self-compatible as ants tend to pollinate within clones but minimises selfing by the elimination of selfed progeny (Peakall & James, 1989). About 60% of visiting ants result in successful pollination (Peakall, 1989).



Fig. 8.9: A male winged *Myrmecia urens* ant positioning itself sideways along the wide labellum of the sexually deceptive *Leporella fimbriata*. Labellum is 10 mm wide. Image provided of Mark Brundrett.

In evolutionary terms, sexual deception may be viewed as a ‘high cost’ strategy as each orchid species obligately deceives a specific pollinating insect, although there is potential for more than one wasp species to pollinate widespread species, as may be the case for sexually-deceptive caladenias (Phillips *et al.*, 2009). It has been argued that the modified floral traits of sexually deceptive orchids have a minimal influence on their pollinator’s evolution (Schiestl, 2005; Jersákova *et al.*, 2006). This is certainly the case for *Cryptostylis* (Fig. 8.8) where all five Australian species are only pollinated by the wasp *Lissopimpla excelsa* (Ichneumonidae), emitting the same chemical attractant (Schiestl *et al.*, 2004) and exhibiting close-range colour mimicry (Gaskell & Herberstein, 2010) but it does not account for the unparalleled diversity and specificity of Thynnine wasp species that pollinate *Drakaea* and sexually-deceptive species of *Caladenia* (Hopper & Brown, 2007; Phillips *et al.*, 2009). Orchid speciation may be a result of subtle changes in the chemical structure of the volatile semiochemicals emitted as a response to speciation rates within their target wasp genera, as has been predicted for *Chiloglottis* species inhabiting the temperate regions of southeastern Australia (Mant *et al.*, 2002; Peakall *et al.*, 2010). Since *Zaspilothynnus nigripes* is the pollinator of *Drakea livida* and several species within the *Caladenia huegelii* complex (Hopper & Brown, 2007; Phillips *et al.*, 2009; Manz *et al.*, 2013), these species probably emit an analogous blend of semiochemicals as their wasp attractant.

8.2 Honeyeater-pollinated Species

Honeyeaters (Meliphagidae) (Fig. 8.10; 8.12) are the main driver of bird-pollination floral traits in the SouthWest flora and the Australian flora in general. Early divergence of honeyeaters occurred 23.5 Ma and radiated strongly between 15 and 5 Ma (Joseph *et al.*, 2014), coinciding with the evolution of the bird-pollinated genus *Leptosema* and radiation of bird-pollinated *Gastrolobium* and *Bossiaea* species (Toon *et al.*, 2014) and hakeas (T. He, unpublished). This represented an evolutionary shift from bee-pollination to bird-pollination syndromes in pea-flowered legumes (Fabaceae, tribes Mirbeliae and Bossiaeae) and hakeas. Similarly, the honeyeater-pollinated genus *Anigozanthos* (Haemodoraceae) originated 14 Ma from insect-pollinated relatives (Hopper *et al.*, 2009) (Fig. 1.1).

Species targeting honeyeater pollinators typically display relatively large, prominent, red-coloured flowers and inflorescences (Fig. 8.10, 8.11) that utilise the bird’s ability to discriminate more towards the red end of the visible colour spectrum (Shrestha *et al.*, 2013), and thus are easily visible among the green foliage and post-fire blackness of the SouthWest vegetation. Prominent flower and inflorescence positioning, including pendulous flowers, have repeatedly evolved in phylogenetically-independent groups to accommodate honeyeaters that need to perch while nectar feeding. An exception to this are the flower heads of *Banksia* (excluding subgenus *Dryandra*) that attract an array of nectar-seeking insects as

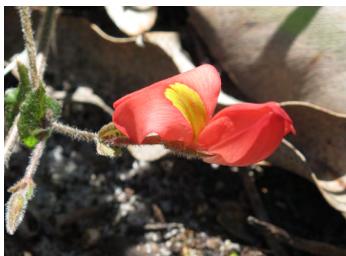
well as honeyeaters (Fig. 8.12). As there are few red-flowering *Banksia* species (e.g. *B. menziesii*; Fig. 7.6; *B. coccinea*, Fig. 8.11), honeyeater visits are a result of learnt foraging behaviours that maximise nectar rewards, with colour-change cues differentiating between unopened and nectar producing florets (Fig. 7.6; 8.12). Honeyeaters feed from the yellow-flowered *B. attenuata* but are not considered its primary pollinators (Wiens *et al.*, 1979; Whelan & Burbidge, 1980).



Fig. 8.10: Examples of honeyeaters that are common in, but not necessarily restricted to, the South West. Brown honeyeater (*Lichenostomus indistinctus*), singing honeyeater (*Lichenostomus virescens*) and white-cheeked honeyeater (*Phylidonyris nigra*). All genera arose 6–8 Ma (Joseph *et al.*, 2014). Birds pictured are 14–20 cm in length, the brown honeyeater being the smallest honeyeater in the SouthWest. (lower left) The floral tube of *Anigozanthos rufus* (Haemodoraceae) is elongated and partially fused as a means of ensuring only honeyeaters are capable of accessing the nectar reward, whereas in *Eucalyptus forrestiana* (Myrtaceae) (middle) the upright yellow stamens create a tunnel-like barrier to nectar seeking insects, but allows access to visiting honeyeaters. (right) *Leptosema daviesioides* (Fabaceae), known as the upside-down pea bush, produces large red flowers from the base of the plant (geoflorous). All flowers 4 cm long. Honeyeater images provided by Geoffrey Groom; floral images by Esperance Wildflowers.



Templetonia retusa
(Fabaceae)



Kennedia prostrata
(Fabaceae)



Leptosema aphyllum
(Fabaceae)



Hakea orthorrhyncha
(Proteaceae)



Hakea laurina
(Proteaceae)



Hakea francisiana
(Proteaceae)



Adenanthos barbiger
(Proteaceae)



Banksia coccinea
(Proteaceae)



Lambertia multiflora
(Proteaceae)



Calothamnus graniticulus
(Myrtaceae)



Eucalyptus rhodantha
(Myrtaceae)



Anigozanthos manglesii
(Haemodoraceae)

Fig. 8.11: Selected examples of bird-pollinated (honeyeaters) flowers in the SouthWest flora showing their great structural diversity. The larger flowers/inflorescences (*B. coccinea*, *E. rhodantha*, *H. francisiana*, *H. laurina*) may also be pollinated by small marsupials such as the honey possum.

SouthWest genera that are considered obligate meliphagiophilous (honeyeater-pollinated) ensure minimal pollen loss to other animal vectors by positioning anthers and stigma in the same location (3–5 cm from the nectar source), even if out-of-phase *via* protandry, to maximise pollen transfer when the bird visits another flower (e.g. *Anigozanthos*, *Leptosema*, *Calothamnus*; Fig. 8.10, 8.11). Other species exclude insect visitors from accessing nectar by imposing impenetrable floral barriers, e.g. *Eucalyptus stoatei* (Hopper & Moran, 1981) and the related *E. forrestiana* (Fig. 8.10), or shield the flowers with conspicuous but dull bracts (e.g. *Pimelea physodes*, Fig. 8.12).

Brush-shaped honeyeater-pollinated flowers are common within the families Myrtaceae, Proteaceae and Fabaceae (Faboideae) (Keighery, 1980) where the pollen is ‘brushed’ all over the bird’s beak and head. Gullet-shaped flowers occur in *Calothamnus* (Myrtaceae), *Anigozanthos* (Haemodoraceae) and some species of *Templetonia* (Fig. 8.11). In all instances visiting birds must reach the nectar at the base of the flower, and in doing so brush pollen onto their heads and beaks.

Distinct bird-pollination syndromes also occur within the Ericaceae (Johnson, 2013). In *Daviesia* (Fabaceae) only two closely-related species are honeyeater pollinated (*D. epiphyllum* (Fig. 9.5) and *D. speciosa*) (Crisp & Cook, 2003, Toon *et al.*, 2014). A full list of bird-pollinated species is provided in Keighery (1980).



Fig. 8.12: Red wattlebird (*Anthochaera carunculata*) (left) sourcing nectar from a pendulous *Pimelea physodes* (Thymelaeaceae) inflorescence, the only bird-pollinated *Pimelea* (Keighery, 1975). Flower head 5 cm long. Western wattlebird (*Anthochaera lunulata*) (right) using the inflorescence of *Banksia speciosa* as a landing platform, feeding from recently opened nectar-producing florets. Western Wattlebird image provided by Lochman Transparencies.

8.2.1 Case Study: *Gastrolobium*

Gastrolobium celsianum (synonym *Brachysema lanceolatum*) (Fig. 8.13) is in the most advanced clade of gastrolobiums and is bird-pollinated (rare among peas) (Crisp, 1996; Chandler *et al.*, 2002; Toon *et al.*, 2014). The clue is the large red flowers, with small standard and wings and abundant nectar. When probed from above

while seeking nectar the bird depresses the keel and initially exposes the anthers (Fig. 8.13, *upper right*) that brush their pollen against the nape and beak and later the receptive stigma receives pollen from the same part of the bird (protandry). Coverage by the keel prevents rainwater washing away the presented pollen. The less advanced species, *G. bilobum*, has dense racemes of small, yellow, insect-pollinated flowers with the standard exceeding the length of the keel. The terminal inflorescence is vulnerable to florivores, such as emus, that have evolved however to withstand the exceptionally high levels of the toxin fluoroacetate, up to 2 mg g⁻¹, that they contain (Twigg *et al.*, 1996; Twigg & Socha, 1996). It is unknown if *G. celsianum* also contains fluoroacetate but the red coloration suggests that they are more likely to contain cyanogenic glycosides to which immunity is unlikely and is a feature of red-coloured, bird-pollinated hakeas and grevilleas for example (Hanley *et al.*, 2009).



Fig. 8.13: *Gastrolobium celsianum* (*upper*) is bird-pollinated, displaying large red flowers, 35 mm long. (*lower*) *G. bilobum* is insect-pollinated, flowers 8 mm long.

8.2.2 Pollen Dispersal

An advantage of utilising honeyeater as pollinators is their ability to carry significant pollen loads over long distances within relatively short time frames (Byrne *et al.*, 2007), although honeyeaters tend to move more frequently between inflorescences on the same plant (Wooller *et al.*, 1983; Collins & Spice, 1986; Day *et al.*, 1997; Byrne *et al.*, 2007). It has been estimated that for hybridisation to have occurred between *Banksia hookeriana* and

B. prionotes the birds must have carried successful pollen for a distance of at least 250 m (Lamont *et al.*, 2003). This is particularly advantageous for trees and shrubs either restricted to specific habitats (e.g. granite outcrops, heathlands) and species with disjunct and fragmented populations. Some prolific post-fire flowering species (e.g. *Anigozanthos* species, *Verticordia grandis*) take advantage of the barren, burnt landscape to attract honeyeaters (Lamont & Downes, 2011). This maximises the incidences of pollen load transfer between flowers within and between populations as honeyeaters need to visit more flowers per species because other species are not in flower. Floral visiting rates are high as honeyeaters continually need to frequently visit nectar-producing flowers to meet their daily energy requirements (Collins & Morellini, 1979; Collins, 1981; Collins & Briffa, 1983; 1985). Honeyeaters utilise multiple plant species, the composition depending on seasonal availability of nectar (Hopper, 1981; 1980), sourcing nectar from adjacent habitats as necessary (Collins, 1985).

Studies on two iconic granite outcrop endemics, *Kunzea pulchella* and *Eucalyptus caesia* (Myrtaceae), have shown that they have a history of population isolation and persistence from at least the Pleistocene. Both possess prominent nectar-laden red flowers that are pendulous in *E. caesia* (see Fig. 7.3 for photograph of *E. caesia* flower). Honeyeater pollination between neighbouring outcrops is a driver of population divergence caused by genetic drift (Moran & Hopper, 1983; Byrne & Hopper, 2008; Tapper *et al.*, 2014). The reliance on honeyeaters is most important for the geographically restricted *E. caesia* because of its inability to inbreed (Byrne & Hopper, 2008) and its protandrous nature. Bird pollination maintains genetic diversity of populations by promoting outcrossing, particularly those that are disjunct and fragmented. This is the case for the rare *E. rhodantha*, despite its low level of outcrossing, where high levels of gene flow between populations maintain relatively high levels of population heterogeneity (Sampson *et al.*, 1989) and also in the outcrop endemic *Kunzea pulchella* (Tapper *et al.*, 2014).

8.3 Mini-possum Pollination

The main marsupial pollinators (therophily) of the South West flora are the minute honey possum (*Tarsipes rostratus*: Tarsipedidae) and western pygmy possum (*Cercartetus concinnus*: Burramyidae) (Fig. 8.14), although rodents (e.g. bush rat, *Rattus fuscipes*: Muridae) may also be active. Mini-possums are the most recently evolved pollinators of the South West flora. Weighing up to 16 g, both species are twilight-active and nocturnal opportunistic foragers for suitable nectar producing and pollen bearing flowers. *T. rostratus* is endemic to the South West and a nectar-feeding specialist, the only non-flying mammal to do so, with a ‘brush’ tongue for lapping up nectar and pollen (Richardson *et al.*, 1986). *C. concinnus* is omnivorous, consuming fruit, seeds, insects and spiders. These mini-possums forage almost exclusively on species with large inflorescences and flowers within the Proteaceae, Myrtaceae and Ericaceae (Hopper,

1980; Bradshaw *et al.*, 2007; Pestell & Petit, 2007; Dundas *et al.*, 2013), widespread in the flora of their heath and woodland habitats. Many of the species visited and pollinated by these mini-possums are also visited by honeyeaters (e.g. *B. coccinea*, *B. baxteri*, *B. occidentalis*) (Hopper, 1980). Mini-possums may be deterred from visiting the large pink-red flowers of bird-pollinated *Hakea* (Proteaceae) species because of the lack of floral scent and presence of floral toxins (cyanogenic compounds) (Hanley *et al.*, 2009). Mammal-pollinated inflorescences are usually not brightly coloured, hidden within the foliage (cryptic), have a strong, often musky, scent and produce copious viscous nectar that may run to the ground as a scent trail.



Fig. 8.14: (upper) Honey possum (*Tarsipes rostratus*), an obligate nectarivore, feeding from *Banksia* inflorescences (left) about to probe *B. benthamiana* that does not present its pollen, (right) probing 20-cm-long flower head of the rare *B. tricuspis* that presents its pollen on hooked styles so that pollen is combed through the possum's fur. It is a highly effective pollinator of *B. tricuspis*. (bottom) Western pygmy possums (*Cercartetus concinnus*) feeding on pollen and nectar from flowers of *Eucalyptus preissiana*, 5 cm wide. Because of the many stamens, pollen is deposited on their snouts, heads and ears. One individual is also using its forelimb to collect pollen. Image of *B. tricuspis* by Stephen van Leeuwen. Other images provided by Lochman Transparencies.

Primarily restricted to a home range up to only 0.8 hectares, with males foraging wider than females, it has been suggested that *T. rostratus* has an intimate knowledge of the local food sources available throughout the year (Garavanta *et al.*, 2000; Bradshaw & Bradshaw, 2002). Nectar is scarce during the dry summer months compared with the winter months (Wooller *et al.*, 1984; Bradshaw & Bradshaw, 1999), with some individuals recorded to move as far as 400 m in search of a suitable food source (Bradshaw *et al.*, 2007).

T. rostratus is the predominant pollinator of many *Banksia* species with hooked styles. Their flowering heads contain hundreds of florets each with recurved styles terminated by a pollen presenter. This transfers pollen to and from the possum's fur as they clamber in search of nectar (Fig. 8.14). Mini-possum-pollinated banksias are typically shrubby and short in stature or prostrate, although both mini-possums have been observed feeding from species that are small trees. Arborescent banksias pollinated by mini-possums (e.g. *B. nutans*, *B. grandis*, *B. tricuspis*) all have pale yellow or brown flower heads often held within the crown rather than displayed prominently as in bird-pollinated species (Table 8.1). Interestingly, disjunct populations of the yellow-flowered *Banksia verticillata*, restricted to granite outcrops on the south coast of the SouthWest, are primarily pollinated by honeyeaters that promote outcrossing. Some mini-possum-pollinated species previously ascribed to the now defunct genus *Dryandra* are ground flowering (e.g., *B. brunnea*, *B. proteoides*; Fig. 7.13) and cryptic (e.g. *B. nivea*, *B. dallanneyi*, *B. plumosa*). Prostrate banksias (*B. goodii* complex) are also ground flowering (geoflorous) with rusty-brown, possum-pollinated, flower heads (Fig. 2.6). It has been speculated that the geoflorous habit in *Banksia* is derived from bird-pollinated ancestors as a means of avoiding the impact of low intensity fires (Rourke & Wiens, 1977) but these species in fact are highly vulnerable to ground fires and they also retain their dead foliage and florets that promote their flammability (He *et al.*, 2011). *Banksia nutans* is a 1-m-tall shrub with pendulous, cryptic, purple-brown, musky, nocturnal-opening flower heads (Table 8.1) whose nectar may drip to the ground and is exclusively pollinated by *T. rostratus* (Wooller & Wooller, 2003). This species has the ability to self-pollinate, a strategy to maintain seed production in the absence of honey possum visits (Wooller & Wooller, 2003).

Mini-possums are unlikely to have had a major evolutionary influence on plant trait adaptation in the SouthWest due to their small size and limitations on their daily energy requirements for travelling long distances. There is also significant competition for limited seasonal nectar resources with the daylight-active, and more mobile, honeyeaters. Nevertheless, some plant species, such as *B. nutans*, have adapted strongly to their ongoing presence over the last few million years.